A QUANTITATIVE STUDY OF ANAPHASE MOVEMENT IN THE APHID TAMALIA

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No single phase of mitosis has been discussed as often as the anaphase movement of chromosomes. The precision of the movement, the relatively large distances covered and the possibility of correlation with definite cellular structures make it better suited for causal analysis than any other phase of cell division. A great number of ingenious hypotheses have been designed to account for the movement of chromosomes, making use of practically every known chemical and physical process which could bring chromosomes from the metaphase plate to the poles. But so far none has been satisfactory and none has been verified even partly by experiment. To some extent this failure is due to the difficulty of the subject. Another reason is the over-emphasis on deductive schemes which may explain a movement of bodies like chromosomes but which are without empirical foundation. This was clearly stated by Bělař (1929a) when he pointed out that we have to find out how the chromosomes move before we can ask what forces are responsible for this movement. What is needed then is a quantitative description of the chromosome movement derived from the study of living cells in division. There are in the literature only two such accounts: one by Bělař (1929a) in spermatocytes of the grasshopper (Chorthippus) and the other by Barber (1939) in Tradescantia staminal hair cells. Bělař derived his data from measurements on photographs which were taken at intervals of several minutes. This can give only a very rough picture of the chromosome movement. Barber measured the distance between disjoining kinetochores, again on photographs, at intervals of one-half or one minute and therefore could offer a more complete description of the anaphase movement. However, the position of the long chromosomes in the metaphase plate and in early anaphase make exact measurements in these stages almost impossible. The present investigation was undertaken to provide more data on the movement of chromosomes in living cells as a basis for both experimental attacks and theoretical interpretations.

Material and Methods

The bearberry aphid *Tamalia coweni* was found to be favorable material for the study of cell division in both spermatocytes and embryonic cells. Several males or parthenogenetic females are dissected in a drop of paraffin oil on a coverglass. The testes—or young embryos—come to lie in a small pool of body fluid surrounded by paraffin oil. The coverglass is then inverted over a depression slide. Cells have thus been kept alive and normally dividing for more than 10 hours. A glass container with ferrous ammonium sulphate between lamp

and microscope prevented any heating due to the light source. The temperature varied from 22° to 26°. A good indication of the normality of conditions is given by the close agreement of the curves of different cells from different individuals (Fig. 1a and 4a). In addition spermatogonia and spermatocytes of *Protenor belfragii* and *Thelia bimaculata* were studied in a hanging drop of paraffin oil.

To analyze the movement of the chromosomes, a metaphase plate in side view is selected and with beginning anaphase the distance between the kinetochores of the daughter chromosomes recorded at intervals of one half to one minute with a camera lucida. This method was found to be simpler and more accurate than measurements on photographs. The error as determined from 20 measurements is ± 4 per cent. The various distances are then calculated in micra and plotted against time (Barber, 1939). We thus get a curve describing the movement of the chromosomes.

All forms studied here are characterized by a diffuse spindle attachment and therefore parallel disjunction. (Hughes-Schrader and Ris, 1941; Ris, 1942). This makes it easier to follow one single chromosome from metaphase to telophase. To avoid the error due to the curvature of the spindle a chromosome near the spindle axis is chosen. As a complement to the studies on live cells fixed and stained sections were used to measure the length of chromosomal fibers as well as the whole spindle with increasing separation of the daughter chromosomes.

The optics used consisted of a 2 mm. Zeiss oil immersion N.A. 1.4 and 15 × ocular.

Anaphase movement in secondary spermatocytes of Tamalia

The type of anaphase movement characteristic for the forms studied is most clearly shown in the secondary spermatocytes of Tamalia (Fig. 1a). When the daughter chromosomes begin to separate they are first connected by a "gray" mass which then breaks up into a few strands. These probably are identical with the Feulgen positive chromosome connections found in fixed cells (Ris, 1942). In a frontal or end view the chromosomes have a very characteristic dumb bell shape. The movement of the chromosomes is slow until all these connections have disappeared. Now it increases in speed and remains nearly uniform for several minutes, when it comes to a halt for about two minutes. The motion is then resumed only to slow down once more as the end of anaphase is approached. The second movement after the plateau in the curve coincides with the elongation of the cell. Previously the cell is spherical or in rare cases has elongated only slightly. Within about ten seconds after the beginning of elongation the cleavage furrow appears (arrow in Fig. 1a).

How can the interruption in the movement of the chromosomes be explained? The coincidence of cell elongation and the second movement of the chromosomes suggests that both may be connected with a stretching of the spindle. We could then picture the anaphase movement as composed of two phases: in the first the chromosomes approach the poles, or in other words, the chromosomal fibers shorten.[1] In the second phase the spindle stretches and moves the chromosomes farther apart. To prove this hypothesis we must take recourse to stained sections

[1] Since nothing is known about the mode of action of chromosomal fibers the term "shortening of chromosomal fibers" is used throughout this paper.

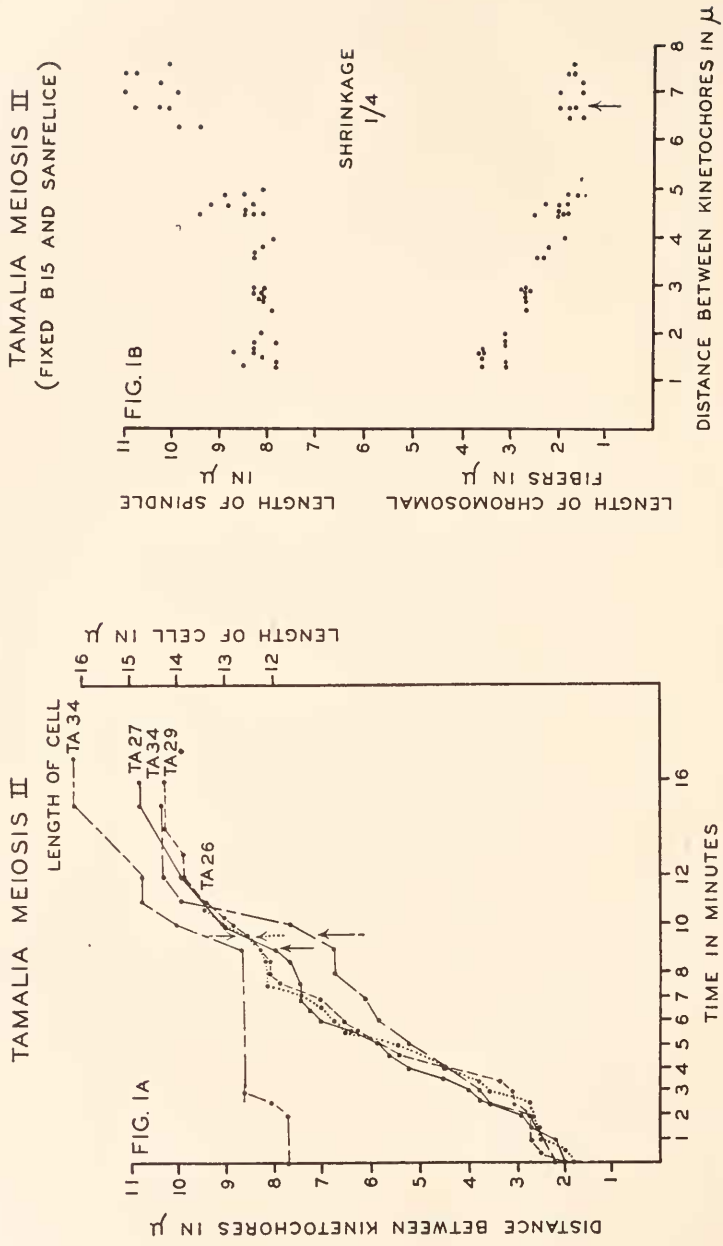


FIGURE 1a and 1b. Chromosome movement in secondary spermatocytes of Tamalia. 1a: measurements on living cells. The arrow marks the appearance of the cleavage furrow. For Ta 34 both distance between kinetochores and length of cell are plotted. 1b: measurements on fixed cells.

where we can measure the length of chromosomal fibers and spindle for various distances between the daughter chromosomes. Such measurements are plotted in Figure 1b. They show clearly that in the first part of the movement the chromosomal fibers shorten while the spindle remains constant in length. In the second phase the chromosomal fibers remain constant while the spindle begins to stretch, causing the further movement of the chromosomes. Making allowance

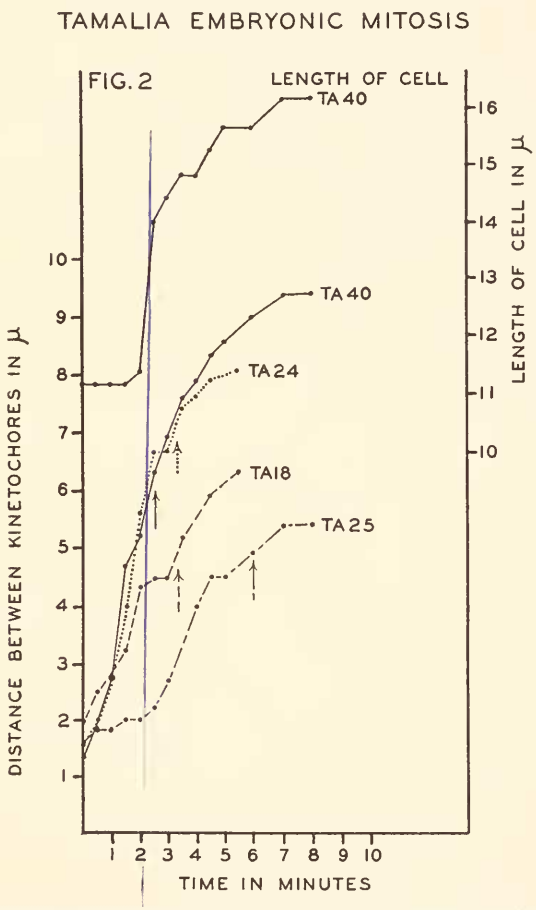


FIGURE 2. Chromosome movement in embryonic cells of Tamalia. Measurements on living cells. For Ta 40 both distance between kinetochores and length of cell are plotted.

for shrinkage at fixation, Figures 1a and 1b can be compared. Shrinkage was calculated by comparing the maximum separation of daughter chromosomes in living and fixed cells and results in a shortening of the interchromosomal distance by one-fourth. In the living cell the break in the curve occurs when the daughter chromosomes are from 7 to 8 μ apart, in the fixed cells accordingly at a separation of 5 to 6 μ. It is also interesting that the elongation of the cell corresponds closely to the increase of spindle length (increase in length of cell 4 μ, of fixed spindle 3 μ).

The movement of the chromosomes in this division can now be described in the following way: first slowly, then faster the chromosomes approach the poles apparently through the action of the chromosomal fibers. When they are from 7 to 8 μ apart this movement ceases and for a short time the chromosomes come to rest. Then the spindle begins to elongate, causing the final separation of the chromosomes. The distance from chromosomes to poles remains constant in this latter phase.

Anaphase movement in embryonic cells of Tamalia

Young embryos dissected from parthenogenetic females have many somatic cells in division. Curves for the anaphase movement are obtained as in spermatocytes. As there are many different types of cells of various sizes the curves differ quantitatively. The character of the movement, however, is the same in all cells and identical with that in secondary spermatocytes (Fig. 2). There is the initial slow movement, the first fast movement, the pause and the second movement coinciding with cell elongation. Because of the difference of

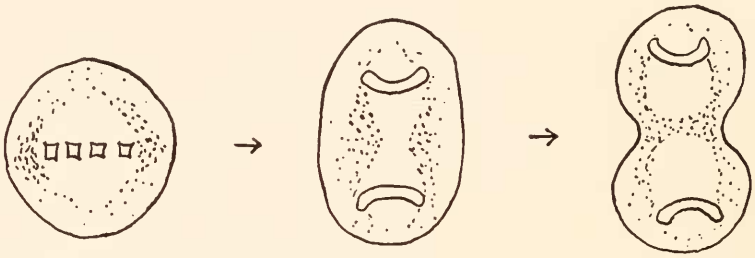
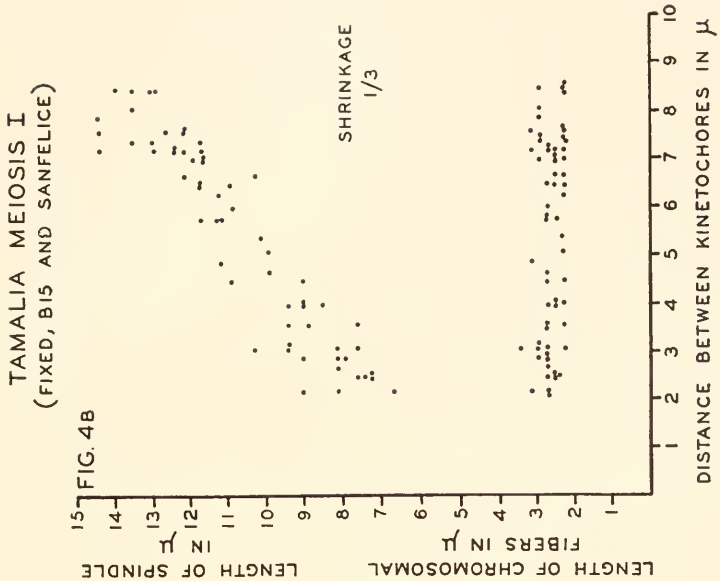


FIGURE 3. Anaphase in embryonic cell of Tamalia. Penetration of cytoplasmic granules in between the daughter plates. See text.

the cells a comparison with measurements of fixed material is impossible. Yet the curves agree well enough with those of secondary spermatocytes to justify the conclusion that the nature of the movement is the same. The velocity of the chromosomes is greater than in spermatocytes and large enough so that the chromosomes can actually be seen in motion under the microscope.

The observation of these cells during anaphase furnishes some interesting data on the spindle. The cytoplasm contains a great number of dark granules of various sizes. When the spindle is formed at metaphase they accumulate along its surface and thus outline its shape. In constant Brownian movement they can be seen bouncing off the surface of the spindle, but never penetrating it. Towards the end of metaphase the majority of granules has accumulated around the equatorial region of the spindle. In the first part of anaphase the spindle retains its characteristic shape, outlined by the cytoplasmic granules. As soon as the cell begins to elongate, indicating the stretching of the spindle, the granule-free region between the daughter plates becomes constricted in the middle and shaped like an hour glass. Soon afterwards cytoplasmic granules rush into the midregion of the spindle, continuously in unrestricted Brownian movement (Fig. 3).



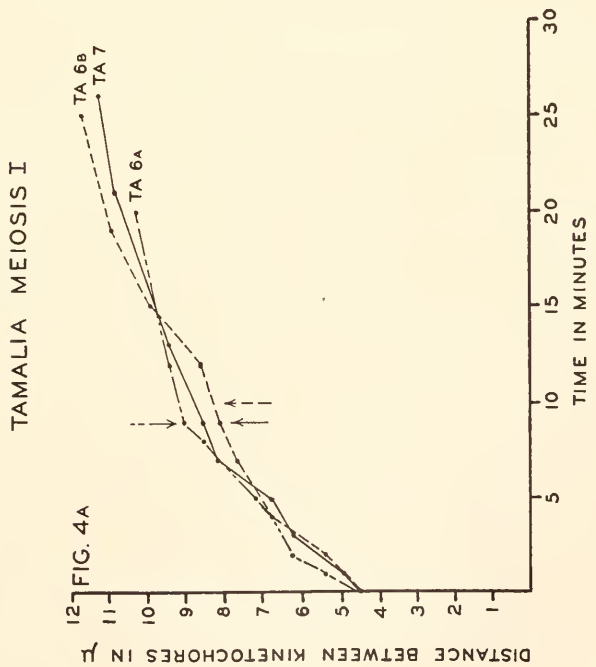


FIGURE 4a and 4b. Chromosome movement in primary spermatocytes of Tamalia. 4a: measurements on living cells. 4b: measurements on fixed cells.

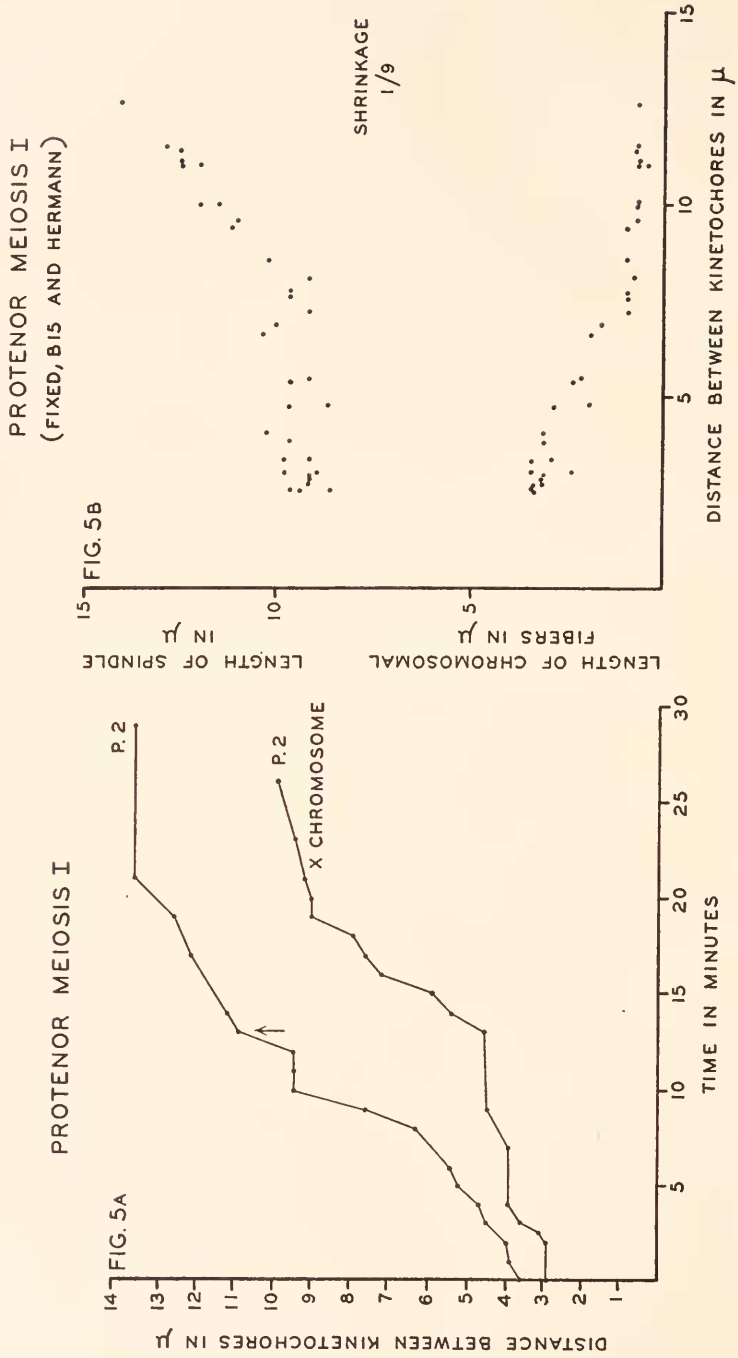


FIGURE 5a and 5b. Chromosome movement in primary spermatocytes of Protenor. 5a: measurements on a living cell, curve for autosomes and lagging X chromosome. 5b: measurements on fixed cells.

Anaphase movement in primary spermatocytes of Tamalia

The first spermatocyte division of the aphid is unusual in several ways. The univalent X chromosome is stretched into a flat sheet at anaphase and passes undivided into the larger of the unequal daughter cells (cf. Ris, 1942).

The anaphase movement also is different from that in cells previously described (Fig. 4a). The chromosomes very soon reach their maximum velocity and then gradually slow down towards the end of anaphase. The curve resembles the second movement in secondary spermatocytes, which was found to be caused by spindle elongation. Indeed the measurements of chromosomal fibers and spindle in fixed cells show that the entire movement of the chromosomes is due to the stretching of the spindle. The chromosomal fibers remain constant in length,

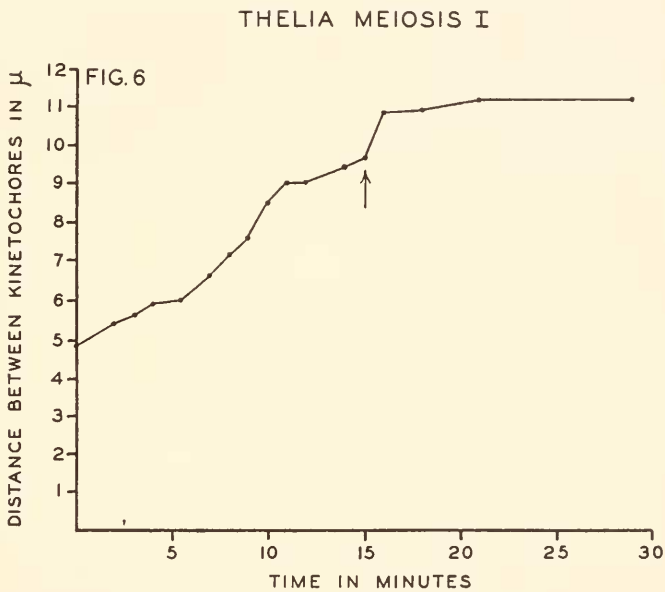


FIGURE 6. Chromosome movement in a primary spermatocyte of Thelia.

i.e., the chromosomes do not get nearer the poles (Fig. 4b). The arrow in Figure 4a marks the appearance of the cleavage furrow.

Is this kind of anaphase characteristic for primary spermatocytes or is it peculiar to the aphid? To answer this question the anaphase movement in primary spermatocytes of the hemipteran Protenor and the homopteran Thelia was analyzed.

Anaphase movement in primary spermatocytes of Protenor and Thelia

The chromosome movement in a primary spermatocyte of Protenor is shown in Figure 5a. The curve for the autosomes is of the same type as those found for somatic mitosis and secondary spermatocytes in the aphid. Again the cleavage furrow appears shortly after the second movement has started. Measurements of

fixed cells finally show that anaphase here too consists of the two phases, the approach to the poles and the spindle elongation.

Interesting is the behavior of the univalent X chromosome. In the first meiotic division it splits equationally but the daughter chromosomes lag behind the autosomes (Schrader, 1935). What is the reason for this delay? The curve for the X chromosome in Figure 5a shows that it is the first part of anaphase which differs from that of the autosomes. Chromosomal fibers are present (Schrader, 1935), but if they are responsible for the movement towards the poles, they are in some way hampered in their function. In the second phase of the movement, which is related to the stretching of the spindle, the X chromosome behaves like the autosomes and even partially catches up with them.

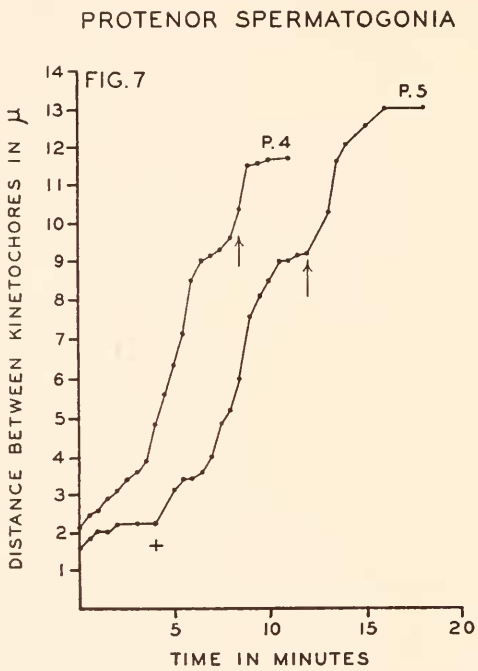


FIGURE 7. Chromosome movement in two spermatogonia of Protenor.

The first meiotic anaphase of Thelia is similar in character to that of Protenor (Fig. 6) and thus also of the same type as found in somatic cells and secondary spermatocytes of the aphid. It must be concluded, therefore, that the anaphase movement of the first meiotic division in Tamalia is different from that in Protenor and Thelia and represents an exceptional case.

Anaphase movement in spermatogonia of Protenor

In Figure 7 the anaphase movement in two spermatogonia of Protenor is recorded. In P_4 the distance between the ends, in P_5 that between the middle of two daughter chromosomes was measured. A comparison of the two curves

shows how the ends of the chromosomes separate first while the midregion lags until the daughter chromosomes are fully separated (+ in P_5). Again the movement consists of two phases, separated by a short pause.

Discussion

The measurements on living cells have furnished curves which describe in detail the movement of the chromosomes at anaphase. In the cells studied it

Table I

Anaphase movement in secondary spermatocytes and embryonic cells of Tamalia.
d.k. = *distance between kinetochores;* l.c. = *length of cell*

	Spermatocytes 11					Embryonic cells				
Time (minutes)	Ta 26 25° C. d.k.(μ)	Ta 27 24° C. d.k.(μ)	Ta 29 24° C. d.k.(μ)	Ta 34 23° C.		Ta 18 24° C. d.k.(μ)	Ta 24 26° C. d.k.(μ)	Ta 25 25° C. d.k.(μ)	Ta 40 22° C.	
				d.k.(μ)	l.c.(μ)				d.k.(μ)	l.c.(μ)
0	1.8	2.0	2.0	2.2	11.7	2.0	1.6	1.6	1.4	11.2
½	2.0	—	2.5	—	—	2.5	2.0	1.8	1.8	11.2
1	2.5	2.2	2.7	—	—	2.7	2.7	1.8	2.7	11.2
1½	2.5	2.7	2.7	—	—	3.2	4.0	2.0	4.7	11.2
2	2.7	2.9	2.7	2.7	11.7	4.3	5.6	2.0	5.2	11.4
2½	2.7	3.8	3.1	3.6	12.1	4.5	6.7	2.2	6.3	14.0
3	3.6	4.0	3.1	3.8	12.6	4.5	6.7	2.7	6.9	14.4
3½	3.8	4.5	3.3	—	—	5.2	7.4	—	7.6	14.8
4	4.5	5.2	4.5	4.5	12.6	—	7.6	4.0	7.9	14.8
4½	4.9	5.6	5.4	—	—	5.9	7.9	4.5	8.3	15.3
5	5.4	5.8	—	5.2	12.6	—	—	4.5	8.6	15.7
5½	6.5	6.3	6.3	—	—	6.3	8.1	—	—	—
6	6.7	7.0	6.5	5.8	12.6			4.9	9.0	15.7
6½	7.0	7.2	—	—	—			—	—	—
7	7.4	7.4	7.0	6.1	12.6			5.4	9.4	16.2
7½	8.1	7.4	7.9	—	—			—	—	—
8	—	—	8.1	6.7	12.6			5.4	9.4	16.2
8½	8.1	7.6	8.1	—	—					
9	—	7.9	8.3	6.7	12.6					
9½	8.5	8.5	8.5	—	—					
10	9.0	9.0	8.8	7.6	14.0					
10½	9.4	—	9.0	—	—					
11	—	—	9.4	9.9	14.9					
12		9.9	9.9	10.3	14.9					
13		—	9.9	10.3	16.2					
14		—	10.3	—	—					
15		10.8	—	10.3	16.2					
16		10.8	10.3							

was found to be composed of two parts. The first can be described as the shortening of the chromosomal fibers which moves the chromosomes towards the poles. The second consists of the elongation of the spindle, resulting in a further movement of the chromosomes.

In general, this picture of anaphase agrees with Bělař's hypothesis which

resolves anaphase into (1) the action of the "Zugfaser" and (2) that of the "Stemmkörper." However, the chromosomal fibers, in the aphid at least, do not attach to a continuous fiber ("Leitfaser"), but form direct connections from the chromosome to the pole. No continuous fibers can be seen in this form. There is also little in favor of a specific differentiation of the region between the daughter-chromosomes into a "Stemmkörper." The intrusion of cytoplasmic granules into the equatorial region of the spindle (page 168) is evidence that this part of the

TABLE II

Anaphase movement in primary spermatocytes of Tamalia (Ta), *Protenor* (P), *and Thelia* (Th). d.k. = *distance between kinetochores*

Time (minutes)	Ta 6a 23° C. d.k.(μ)	Ta 6b 23° C. d.k.(μ)	Ta 7 25° d.k.(μ)	P 2 25° C.		Th 1 25° C. d.k.(μ)
				autosomes d.k.(μ)	X chromosome d.k.(μ)	
0	4.5	4.5	4.5	3.6	2.9	4.9
1	4.9	5.4	4.9	3.8	—	—
2	5.4	6.3	—	4.0	2.9	5.4
2½	—	—	—	—	3.1	—
3	—	—	6.3	4.5	3.6	5.6
4	6.7	6.7	—	4.7	3.8	5.8
5	—	7.2	6.7	5.2	—	—
5½	—	—	—	—	—	6.0
6	—	—	—	5.4	—	—
7	7.6	—	8.1	—	3 8	6.7
8	—	8.5	—	6.3	—	7.2
9	8.1	9.0	8.5	7.6	4.5	7.6
10	—	—	—	9.4	—	8.5
11	—	—	—	9.4	—	9.0
12	8.5	9.4	—	9.4	—	9.0
13	—	—	9.4	10.8	4.7	—
14	—	—	—	11.2	5.4	9.4
15	9.9	—	—	—	5.8	9.7
16	—	—	—	—	7.2	10.8
17	—	—	—	12.1	7.6	—
18	—	—	—	—	7.9	10.8
19	10.8	—	—	12.6	9.0	—
20	—	10.3	—	—	9.0	—
21	—		10.8	13.5	9.2	11.2
23	—		—	—	9.4	—
25	11.7		—	—	—	—
26			11.2	—	9.9	—
29				13.5		11.2

spindle is not a rigid "Stemmkörper," but rather less viscous than the rest of the spindle. It is more likely that the spindle as a whole elongates, though probably to a greater extent in the equatorial region. Only actual measurements can clarify this point.

The shape of the chromosomes at anaphase indicates that the chromosomal fibers exert a pull on the kinetochore. This is not only seen when the chromosomal fibers shorten and bring the chromosomes to the poles, but also in the first

spermatocyte of Tamalia where spindle elongation alone moves the chromosomes. The motion is therefore transmitted from the spindle to the chromosomes through the chromosomal fibers. The elongating spindle then does not push the chromosomes apart, but separates the poles. The chromosomal fibers, which in some way must be anchored to the polar regions then begin to pull at the spindle attachments of the chromosomes (cf. Ris, 1942; Fig. 84–90).

In the aphid, Protenor, and Thelia the two components of the anaphase movement are completely separated in time. How far can this type of movement be generalized? Barber (1939) in staminal hair cells of Tradescantia found simple S-shaped curves. He drew similar curves also through the points furnished by Bělař's photographs of anaphase in spermatocytes of the grasshopper (Chorthippus). Bělař's points are, however, so far apart that the lines drawn through them are purely hypothetical; they may or may not be simple. In

TABLE III

Anaphase movement in spermatogonia of Protenor. d.k. = *distance between kinetochores*

Time (minutes)	P 4 25° C. d.k.(μ)	P 5 25° C. d.k.(μ)	Time (minutes)	P 4 25° C. d.k.(μ)	P 5 25° C. d.k.(μ)
0	2.2	1.6	8	9.7	5.2
½	2.5	1.8	8½	10.3	6.0
1	2.7	2.0	9	11.5	7.6
1½	2.9	2.0	9½	11.5	8.1
2	3.1	2.2	10	11.7	8.5
2½	3.4	—	10½	—	9.0
3	3.6	2.2	11	11.7	9.0
3½	3.8	—	11½		9.2
4	4.9	2.2	12		9.2
4½	5.6	—	13		10.3
5	6.3	3.1	13½		11.7
5½	7.2	3.4	14		12.1
6	8.5	3.4	15		12.6
6½	9.0	3.6	16		13.0
7	9.2	4.0	18		13.0
7½	9.4	4.9			

Tradescantia staminal hair cells, as in other somatic plant cells, there is no elongation of the spindle and cell (cf. Bělař's photographs, 1929b). We may compare therefore this entire anaphase movement with the first part of that in the aphid. In both cases rather flat S-shaped curves are found. For the grasshopper preliminary measurements have shown that the chromosome movement differs from that of the aphid since the spindle begins to elongate before the shortening of the chromosomal fibers is completed.

The anaphase curve with a distinct separation of the two components is found in three Hemiptera and Homoptera, but in no other form analyzed so far. One may therefore assume that it is related to the special kind of spindle apparatus found in these forms, namely, the diffuse spindle attachment. Should this be confirmed by further studies on other forms it would give additional evidence for the functional importance of structures like chromosomal fibers still believed by

some investigators to be artifacts. It would also be an interesting example of how variations in cellular processes are related to differences in structure.

The behavior of the X chromosome in the first spermatocyte of Protenor is of great interest. Chromosomal fibers are present in metaphase and anaphase, but, as the analysis of the movement in a living cell shows, they are hindered in their normal functioning so that the X chromosome lags behind the autosomes on its way to the poles. This provides a mechanism for individual movements of chromosomes. A similar condition may be responsible for the lagging of specific chromosomes in elimination divisions of Sciara, Oligarces, etc.

The velocity of the chromosomes at anaphase is of great interest. The maximum velocities in the various divisions studied are brought together in table IV. The velocities due to the shortening of the chromosomal fibers and spindle elongation are recorded separately. The greatest velocity in embryonic cells of

Table IV

Maximum velocities of chromosomes. Micra/minutes. 23–26° C.

	Somatic mitosis		Spermatogonia		Meiosis I		Meiosis II	
	chromosomal fibers	spindle	chromosomal fibers	spindle	chromosomal fibers	spindle	chromosomal fibers	spindle
Tamalia	0.7–2	0.3–1.1			—	0.3	0.9–1.2	0.4–1.1
Protenor			1.3–1.6	0.3–0.5	0.9	0.7		
Thelia					0.4	0.5		
Tradescantia (Barber 1939)	1.2 (20° C.)							

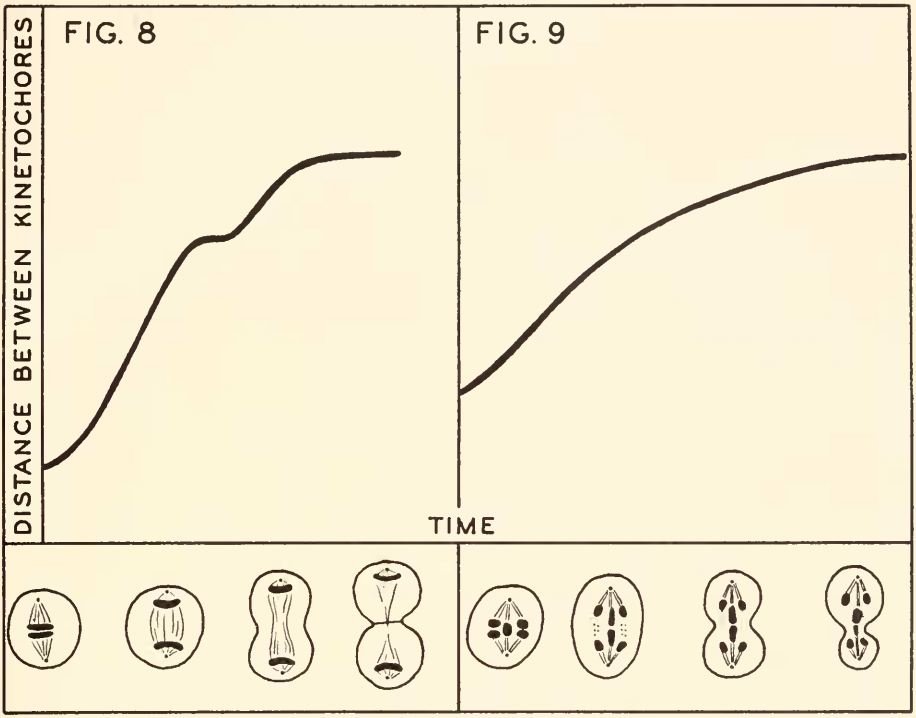
Tamalia is 2 μ per minute, or about 3 mm. in 24 hrs. As comparison the maximum velocity in Tradescantia staminal hair cells reported by Barber (1939) is added to the table.

Conclusions

The character of the chromosome movement at anaphase varies in different groups of organisms. It is possible to describe these differences as modifications in the behavior of components of the mitotic apparatus, such as chromosomal fibers and spindle body. Thus in Tradescantia staminal hair cells there is only the movement to the poles, in the first meiotic division of Tamalia only the elongation of the spindle (diagram Fig. 9). In regular divisions of Hemiptera and Homoptera the action of chromosomal fibers and spindle elongation are separated in time (diagram Fig. 8), in the grasshopper, however, they act simultaneously. These functional differences are correlated with variations in the spindle structure (diffuse against localized spindle attachment).

Measurements of chromosome movement such as those reported by Barber (1939) and in this paper represent a first step in the analysis of anaphase, namely

a quantitative description of the processes observed in the cell. The movement must then be separated into its components and related to the cellular structures which are found to be essential for regular separation of chromosomes (kinetochore, chromosomal fibers, spindle, etc.). A theory of chromosome movement must be



TAMALIA EMBRYONIC CELLS
TAMALIA SECONDARY SPER—MATOCYTES
PROTENOR SPERMATOGONIA
PROTENOR PRIMARY SPER—MATOCYTES
THELIA PRIMARY SPERMATO—CYTES

TAMALIA PRIMARY SPERMATO—CYTES

FIGURES 8 and 9. Diagrams illustrating the chromosome movement in forms with diffuse spindle attachment. 8: the typical anaphase curve. 9: the exceptional curve in primary spermatocytes of Tamalia.

established first on a biological plane, accounting for the many modifications of anaphase as variations of these mitotic organelles. Finally an experimental analysis of the nature of these structures and the changes they undergo during mitosis can provide an empirical basis for a physico-chemical theory of mitotic movement.

Summary

1. The movement of chromosomes at anaphase was measured in living cells of Tamalia, Protenor and Thelia. The distance between the separating chromosomes plotted against time produces curves which describe accurately the chromosome movement. In embryonic cells and secondary spermatocytes of Tamalia, spermatogonia and primary spermatocytes of Protenor, and a primary spermatocyte of Thelia the curves consist of two S-shaped components separated by a plateau. The second part of the movement coincides with the elongation of the cell.

2. In stained sections the length of chromosomal fibers and the spindle was measured at various stages of chromosome separation. A comparison with the data from living cells shows that in the first part of anaphase the chromosomal fibers shorten, i.e., the chromosomes approach the poles. In the second part the spindle elongates and thus produces a further movement of the chromosomes.

3. The chromosome movement in the otherwise exceptional anaphase of primary spermatocytes in Tamalia is characterized by a simple unbroken curve. Measurements on stained cells demonstrate that the movement is due entirely to spindle elongation. The chromosomal fibers remain constant in length and the chromosomes therefore do not approach the poles.

4. Since the double curve was found in all Hemiptera and Homoptera studied but not in the grasshopper (unpublished results) this type of anaphase movement is probably related to the diffuse spindle attachment found in these insects. This points out the functional significance of structural variations.

5. The curves for the primary spermatocyte of Protenor show that the lagging of the daughter chromosomes of the univalent X chromosome is due to an abnormal first part of the movement. This indicates some impairment in the functioning of their chromosomal fibers. The exceptional behavior of a chromosome can thus be traced to one particular factor of the anaphase movement.

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